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On "Darwinian Mysteries" or molluscs as models in evolutionary biology: From local speciation to global radiation*

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Abstract: Evolutionary biology is not only a biological subdiscipline but also a synthetic theory based on comprehensive scientific achievements. However, to date biodiversity, which is far from being fully documented, and the evolutionary processes leading to it are two of the least understood phenomena in evolutionary biology. Surprisingly, decades after the Modern Synthesis and centuries after the commencement of research in biological systematics, we are still unable to satisfyingly answer apparently simple yet fundamental questions. Here termed "Darwinian mysteries", these are for example, how many species inhabit Earth today, what are species, where are they distributed, and how did biodiversity originate. While many contributions in malacology center around morphology, anatomy, and phylogenetic relationships within and among constituent taxa, molluscs only rarely have been utilized explicitly as models for the study of general aspects in evolutionary biology. However, this particular group, with its many features and facets, is highly suitable for providing fundamental insights into the mechanisms that generate biodiversity, pattern in historical biogeography, and the underlying processes of speciation and radiation. Here, I discuss some aspects of these fundamental questions that are of relevance for evolutionary biology, hoping that the influence of malacology within evolutionary biology will increase in the future.

Key words: biodiversity, evolution, species, species numbers, species concepts

> *"Science is built of facts as a house is built of bricks; but an accumulation of facts is no more science than a pile of bricks is a house."*
>
> Henri Poincare, *La Science et l'hypothèse* (1902: 101)

Molluscs are not only one of the most spectacular animal phyla with great taxonomic diversity and morphological disparity but also have the potential to provide us with some of the most remarkable models in evolutionary biology. Actually, it has escaped many (and not only) malacologists' attention that molluscs were at the forefront of evolutionary theory in the first place. For example, they were instrumental in Jean-Baptiste de Lamarck's (1744-1829) first evolutionary views. When Lamarck (1801) introduced his then novel classification of invertebrates and included Mollusca as a class on its own, based on his study of the rich molluscan collection in the Paris museum, he also proposed in his introductory "*discours préliminaire*" a brief exposition of his later, much-debated evolutionary theory (Mayr 1982, Schilling 1989, Burkhardt 1995, Laurent 1997). Although Lamarck suggested an incorrect mechanism for evolution, in comparing fossil molluscs with recent species, he for the first time realized divergent evolution over geological time scales.

Molluscs were also the trigger, albeit not the focus, of one of the most famous controversies in the history of science, as it was the debate on cuttlefish anatomy that started the epochal debate in the Paris Academy of Sciences in 1830. Here again a group of molluscs was at center stage when Georges Cuvier's functionalism opposed Étienne Geoffroy Saint-Hilaire's "philosophical" morphology (Appel 1987, Le Guyader 2004).

Nevertheless, after this crucial epoch, malacology did not remain at the forefront of zoological discoveries and evolutionary biology. Although being little more than a marginal note in the history of science, to my view the following episode is not only a curious incidence but also a symptomatic indication for our field. Remarkably, not a professional naturalist or scientist with a keen interest in malacology, but the American poet Edgar Allen Poe (1809-1849) was among the first to recognize and comment that a reliable classification of molluscs requires a combined analysis, which meant in his times reconciling a system based on hard shells (as suggested by Lamarck) with evidence from soft body anatomy (as provided by Cuvier). Illustrated by 215 shells of molluscs, Poe (1839) published a scholarly and most successful textbook with a telling title, viz. *The Conchologist's First Book: or, A*

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system of Testaceous Malacology, arranged expressly for the use of schools, in which the animals, according to Cuvier are given with the shells, a greater number of new species added and the whole brought up as accurately as possible to the present condition of the science. And he explicitly distinguished between conchology as being merely the study of shells versus malacology as being the study of molluscs, *i.e.*, the anatomy of the whole animal including its most important soft parts.

After Myra Keen (1936) and Joseph Moldenhauer (1971) had remarked on this case of "literary curiosity", the late Stephen Jay Gould (1993, 1995), both a malacologist and evolutionary biologist himself, looked into this episode in more detail. Gould developed the argument that, irrespective of the plagiarism and piracy of Thomas Brown's earlier book, and Poe's functioning as a ghost writer and straw man for Thomas Wyatt (as is true for one other case; see Heartman and Canny 1943), it was indeed Poe himself who made the above mentioned important distinction. Although published under Poe's name, the book was essentially a less-expensive edition of Thomas Wyatt's (1838) own work *Manual of Conchology*, which plagiarized most of the text from British naturalist Thomas Brown's (1833) *Conchologist's Text-book*. However, since Poe evidently wrote the preface and introduction, then used the system of classification from Wyatt's work, but substituted for each genus a paragraph description of the soft parts (maybe taken over from Cuvier), it can be reconstructed that indeed it was Poe's own novel idea of a combined analysis.

Evidently, his early insight into what malacology should be was not borrowed from either Brown and/or Wyatt. Therefore, it remains a curious fact that Poe as a poet with only a marginal interest in science formulated an explicit conceptual reform (*i.e.*, the distinction between conchology and malacology), apparently an idea with much future. Poe's *Conchologist's First Book*, therefore, should be perceived now as more than just a literary curiosity and a collage from others' texts, as his emphasis of the eminent importance of anatomical features in the distinction and classification of molluscan species reveals innovative potential long unrecognized, paving the way toward malacology as a truly biological discipline.

Unfortunately, his insight was ignored for almost another century while conchologists continued to classify molluscs exclusively based on features of their shell while neglecting the soft body and biological information that it holds. Interestingly, following Lamarck's (1792) earliest attempts on classification of invertebrates, where the systematics of molluscs was solely based on shells, Lamarck (1809) later learned from Georges Cuvier's studies on soft-body anatomy, and acknowledged explicitly the importance of these morphological data for his classification (Corsi 1988: 62). Unfortunately, although Lamarck's classification of invertebrates in his original seven-volume *Histoire Naturelle des Animaux sans Vertèbres* (Lamarck 1815-1822) was widely known and used by many 19th century naturalists, his theoretical insights and reference to Cuvier's attempt were largely ignored. Continuing in this unhappy tradition, students of molluscs for a long period missed the chance to modernize malacology as a scientific discipline. The problem inherent to the traditional study of only shells, for example, for systematic-taxonomic purposes was that no other sources of information were utilized to evaluate the diagnostic value of shell features. This stands in stark contrast to other disciplines like ornithology, where the so called "*new systematics*" provided the foundation for developing the modern theory of evolution (see Glaubrecht 2007, references therein). In the context of malacology developing as a biological science, a study of systematics vs. merely "stamp collecting" (Glaubrecht 2004: 117), I add here as surely more than coincidence that one of Britain's former leading conchologists, Francis James Stainforth (1797-1866), who was a supplier of many rare shell specimens to Lovell Reeve, also initiated in the early 1860s in London the first stamp collector's club, thus helping to found philately (Allen 2008).

However, molluscs are much more than only collectors' items. With their many features and facets, they are highly suitable for providing some fundamental insights into the mechanisms of the genesis of biodiversity, its pattern in historical biogeography, and the underlying processes of speciation and radiations. As recently summarized by Ponder and Lindberg (2008), with about 200,000 living species the Mollusca are one of the largest animal phyla, second only to the arthropods. The remarkably rich fossil record of molluscs enlightens the earliest Cambrian revolution some 540 million years ago, and ever since we find them in nearly every ecosystem on Earth. The seven or eight classes of living molluscs plus two extinct class-rank taxa comprise an array of most diverse animals with most varied body plans, ranging from minute worm-like animals dwelling between sand grains on the beach to giant squids in the deep sea, and from microscopic snails in leaf-litter to giant clams in coral reefs. As objects of fascination, function, and food, molluscs play important roles in many cultures and societies. Molluscs include many taxa of immense economic significance, such as oysters, scallops, and squids; some bivalves produce precious pearls, and some snails carry diseases that infect millions of people, especially in the tropics.

Yet, for a long time we knew few hard facts, for example, about the evolution and phylogeny of these soft-bodied animals. For the greater part of the last century, it was Johannes Thiele's (1929-1931) epochal *Handbuch der Systematischen Weichtierkunde* that long provided the standard in molluscan systematics. For his classification, Thiele evaluated characteristics from the shell but consequently used a synthetic, albeit pre-cladistic manner when he included the

most important radula features as well as other anatomical characters following a tradition started by Troschel (1856-1863). Although Thiele sometimes erred, for example when he discarded aplacophoran molluscs as "worms" belonging to the phylum Annelida (see Glaubrecht *et al.* 2005), his systematization was a highly influential masterpiece. Another curious fact was that when Thiele's handbook was translated into English and re-published by Bieler and Mikkelsen (1992), a substantial amount of new data from both morphology and molecular genetics as well as from paleontology had begun to accumulate, too diverse for a single malacologist to master.

New tools—such as fluorescence-coupled antibody staining and confocal laser-scanning microscopy, in concert with new approaches such as computer-assisted cladistics, which allow the recurrent testing of phylogenetic hypotheses under various models and assumptions—have generated a renewed interest in reconstructing evolutionary history with molluscs in a key position (Valentine 2004, Minelli 2009a). Consequently, within the last two decades our understanding of molluscan phylogeny has undergone a remarkable, if not even revolutionary, transformation that is about to change fundamentally the classification of phyla. Ponder and Lindberg (2008) provide a collation badly needed when virtually every phylogenetic tree calculated from another partial gene fragment of more or less randomly represented taxa is considered publishable.

While many contributions center on morphology, anatomy, and phylogenetic relationships within and among constituent taxa, molluscs have only rarely been utilized as general models for the study of evolutionary biology. Molluscs rarely make it into textbooks on evolutionary theory, and are highly underrepresented when it comes to discussing evolutionary concepts and/or phenomena by example (Ridley 1996, Futuyma 1997, Mayr 2001, Barton *et al.* 2007). For only one more recent example, in a very readable book on evolutionary pathways by Avise (2006), only two cases (coiled vs. uncoiled shells and land snail chirality) explicitly referred to recent studies utilizing molluscs. Undoubtedly, however, molluscs have so much more to teach us.

As evolution is the vibrant foundation for biology, evolutionary biology in this context has a double function. It is not only a biological subdiscipline but also a synthetic theory and discipline on its own, based on comprehensive scientific achievements. Unfortunately, malacologists in particular have followed one of the most prevailing methodological claims that gathering facts should be the primary role of naturalists (Johnson 2005) which often discourages explicit references to evolutionary theory. In addition, as taxonomy and systematics once marked the beginning of zoology in general, it is still among the primary interests of many malacologists. My point is that malacology has more potential to contribute to evolutionary biology than previously assumed or revealed. Taxonomy, albeit not experimental, does not have to remain merely descriptive, but should be hypothesis-driven as well as drive hypotheses. It forms an integral part of evolutionary biology, as taxonomic facts are a prerequisite to the proper formulation of evolutionary and ecological questions (May 1992, 1999).

However, although systematics continues to lay the foundation for many disciplines of the life sciences, its ultimate goals of providing an inventory of biodiversity, and reconstructing a tree of life (Glaubrecht 2007), are far from being achieved in general or in molluscs in particular. The *diversity* of organisms, and the morphological *disparity,* as well as the evolutionary processes leading to it, are the least understood phenomena in evolutionary biology. Some facts and reasons why biological diversity is far from being discovered, or its origin understood, will be briefly highlighted here.

THE SIX "DARWINIAN MYSTERIES" IN BIOSYSTEMATICS AND EVOLUTIONARY BIOLOGY

A love of science has much to do with its mysteries that drive basic scientific research; questions are often considered more important than answers in shaping the future of science and its disciplines. Fundamental questions can be used as guidelines for future, cutting-edge research and reveal opportunities to be exploited, starting from the supposition that scientists should answer these questions over the next quarter century (Kennedy and Norman 2005). In this context, the apparently simple question "What determines species diversity?" was recently ranked among the 25 "big" questions, based on how fundamental they are, how broad-ranging, and whether their solutions will impact other scientific disciplines (Pennisi 2005). Among the others were how Earth's interior works, the composition of the universe, and whether we are alone in it, or whether the laws of physics can be unified.

Highlighting our scientific ignorance, it is surprising that centuries after the commencement of research in biological systematics and decades after the Modern Synthesis of evolutionary biology, we are still unable to answer a series of simple questions linked to this big question on biological diversity. Today, 300 years after Carl Linnaeus (1707-1778) and 200 years after Charles Darwin (1809-1882), both biosystematics and evolutionary biology are still left with the following six "Darwinian mysteries" (Glaubrecht 2003, 2004, 2005, 2007). One and a half centuries after *On the Origin of Species* by Darwin (1859), these questions, all relevant to his (r)evolutionary theories, are all largely unanswered, irrespective of the many fruitful attempts to solve them.

(1) Species numbers: How many species are there?

(2) Species concepts: What are species and how do we know?
(3) Speciation: How do new species evolve?
(4) Biogeography: Where are the species and why are they distributed there?
(5) Phylogenetics: How are species (groups) related?
(6) Genetic causation and molecular processes: How do new forms come into being?

Undoubtedly, answering these questions will ultimately help to unravel some of the most important issues not only in biosystematics, but also in evolutionary biology. To accomplish modern systematists' tasks, viz. quantifying biodiversity, establishing phylogenies, and understanding the evolutionary process of speciation and radiation, several prerequisites are indispensable, albeit neglected even in many modern systematic approaches. Malacology, with one of the richest animal phyla at hand, both in terms of species numbers and biological phenomena, can have its share in solving these "Darwinian mysteries". I outline here only the first three of these Darwinian mysteries in more detail.

(1) The mystery of species numbers: A Linnean enterprise

As taxonomy and systematics provide the reference system for all biology (Wilson 1989), compiling, organizing, and updating taxonomic information has an urgent priority. After decades of de-emphasizing biosystematics (Whitehead 1990, Mikkelsen and Cracraft 2001), and recent taxonomic modernization and renaissance (*e.g.*, Godfray 2002, 2007, Mallet and Willmott 2003, Wheeler 2004, Dayrat 2005, Glaubrecht 2007), the reawakening interest in taxonomy has also led to realization that most animal species, especially invertebrates like molluscs, are far from being discovered yet.

In fact, it can be called the "Linnean shortfall" that, while knowing how many atoms are in a molecule, how many craters are on the moon, and how many stars are in the Milky Way or galaxies in the universe, we still have not learned how many species of butterflies live on tropical trees, how many buccinid gastropods are in the sea, freshwater melanopsids around the Mediterranean, or camaenids in Australia. For way too long a period of time, zoologists seemed to perceive "a number of undescribed creatures rather a nuisance", as Darwin long ago complained (Keynes 2003). Nearly three centuries after Linnaeus's first attempts to inventory nature, his task remains a daunting challenge for systematists, including malacologists.

Surprisingly, only recently has it become apparent that we lack the most fundamental data on biodiversity, viz. systematic inventories on any organismal, ecological, and geographical level (*e.g.*, Wilson 1988, 1992, Raven and Williams 1997, for molluscs see Bouchet 1997). Recognizing and describing the living species of plants and animals on Earth, however, is a major task, calling for a large-scale approach to taxonomy (Raven and Wilson 1992, Wilson 2000, 2003, Lawler 2001, Mikkelsen and Cracraft 2001, Blackmore 2002, Wheeler *et al.* 2004, Stork 2007), comparable to the Human Genome Project or the NASA next generation space telescope and Sloan Digital Sky Survey. Indeed, it remains an unfinished Linnean challenge to inventory the many species that exist on Earth.

Estimates of the number of living species in the world, given by Terry Erwin (based on neotropical insect diversity) as up to 30 million species, have triggered more specific attention, as the question 'How many species are there?' has finally been regarded as scientifically important (Erwin 1982, May 1988, 1990, 1992, 1994, 1999, Stork 1988, 1993). Estimates of the total number of species vary now from 5 to over 50 million, using various direct and indirect assessments. Over the last two decades, these global estimates dropped to a total of 5 to 15 million species (Stork 1993, Odegaard 2000). A most comprehensive compilation of species numbers has been provided by Chapman (2005), who settled on between 8 and 9 million species.

In this context, the discussion has largely centered around the question of what fraction of the insect species found on a given host-tree is likely to be effectively specialized on it, on species-size relations, or in food web structure (May 1990). For example, after having taken into account the host specificity in particular of herbivorous insects, which is essentially responsible for driving most of these species number estimates, the figure has recently been corrected to 4.8 to 6.6 million species (Novotny *et al.* 2002, 2007). The latter authors attempted to reconcile an order of magnitude discrepancy between extrapolations based on ecological samples with those based on sampling regional faunas or estimates based on taxonomic collections. However, it is doubtful that neotropical, herbivorous insect diversity is a direct function of plant species number (comprising taxonomic and architectural diversity), suggesting that additional factors like the existence of morphologically cryptic species and distributional ranges would again increase global species numbers (Dyer *et al.* 2007, Condon *et al.* 2008). Surprisingly, very little solid data has been contributed to the discussion of species richness from other invertebrates, such as molluscs or for aquatic biota, with the notable exception of Bouchet *et al.* (2002) for marine molluscs, that may account for a large fraction of all marine invertebrate species. Therefore, not even the magnitude of the world's diversity is currently known to systematists, let alone exact figures for particular groups of animals. Although it is agreed now that we desperately need a biodiversity assessment comprising a complete inventory of life, we are still challenged to develop rough estimates on the quantity of species as the units of biodiversity studies and evolution (see below).

Irrespective of a more exact estimate of the number of species, we are faced with a tremendous task, given that only

approx. 1.8 million animal species have been properly described (Stork 1988, May 1990). Amazingly, not even the number of species that have already been named and recorded is known precisely. Thus, not only does Linnaeus lag so far behind Newton (given our knowledge about the universe compared to the living world), but more importantly at the level of individual taxonomic groups we see major differences in the accumulation of recorded numbers of known species, with most invertebrate groups being largely underexplored. May (1990, 1992) has calculated the rate of discovery from the times of Linnaeus (1758) up to 1970 and 1990, respectively. In Fig. 1, vertebrates are illustrated by the most representative group, birds, versus an invertebrate group, arthropods. Expressed as a fraction of those species known in 1990, half of all known bird species were already recorded in the century after Linnaeus, by 1845. In contrast, only half of the arthropods known in 1990 were described within the preceding three decades. The "furries and featheries" are very well known by now, at least at the genus level, with only 134 bird species being added to the total of over 9000 since 1934 (Diamond 1985) and only a few mammal species. With respect to invertebrates (including, of course, molluscs, see below), we have just started to deal with the Linnean challenge of a species inventory.

We also have to face the fact that most biological assessments largely use focal groups, *i.e.*, vertebrates and vascular plants, but few invertebrate groups such as butterflies. They all comprise not more than five percent of the known diversity while major environmental players (bacteria, fungi, mites, nematode worms, and beetles) are largely unknown, underrated, and underestimated (May 1988, 1992). The major part of diversity in most invertebrates, the other 99% as it has been called (Ponder and Lunney 1999), is therefore still hidden. In Fig. 2 the most recent figures for individual animal groups used by Chapman (2005) is shown, giving the number of known and of estimated species, respectively, for Mollusca as 70,000 to 120,000 species. Other figures of the number of described species of invertebrates were in the past rightly criticized for not only being a matter of great difficulty but also of little value, and those in most textbooks of zoology were long simply copied from each other. Currently, only a few studies are available for global estimates of specific taxonomic groups, such as (1) arthropods and more specifically Hymenoptera (Odegaard 2000, Dolphin and Quicke 2001), (2) on some crustaceans trying to also quantify the underestimation (Adamowicz and Purvis 2005), or (3) on marine fishes (Mora *et al.* 2008). However, how much do we as malacologists know about the various subjects of our special interest among the marine, freshwater, and terrestrial taxa? With the world's oceans and tropical rain forests teeming with life forms, each new survey increases the window through which we see this living world. Our museum collections are already filled with nearly endless numbers of scientific hypotheses, biological tests, and questions. However, can we hope that we will eventually understand the biosphere if we do not even struggle to make comparable inventories of our knowledge on these new and old discoveries?

It is estimated that we currently add roughly 10,000 new animal species each year (May 2004), among which are well over 400 new species of Mollusca (Bouchet 1997), discounting for past synonymies (see discussion below). With this plethora of new species and taxa continuously being found, however, we do not even attempt to list how many new species *exactly* are described annually, or how many await description. Yet we lack, curiously enough, several of the most important parameters or instruments to compile a complete list of species on Earth. To begin with, we still have an incomplete taxonomic database for the known species in the world, as no

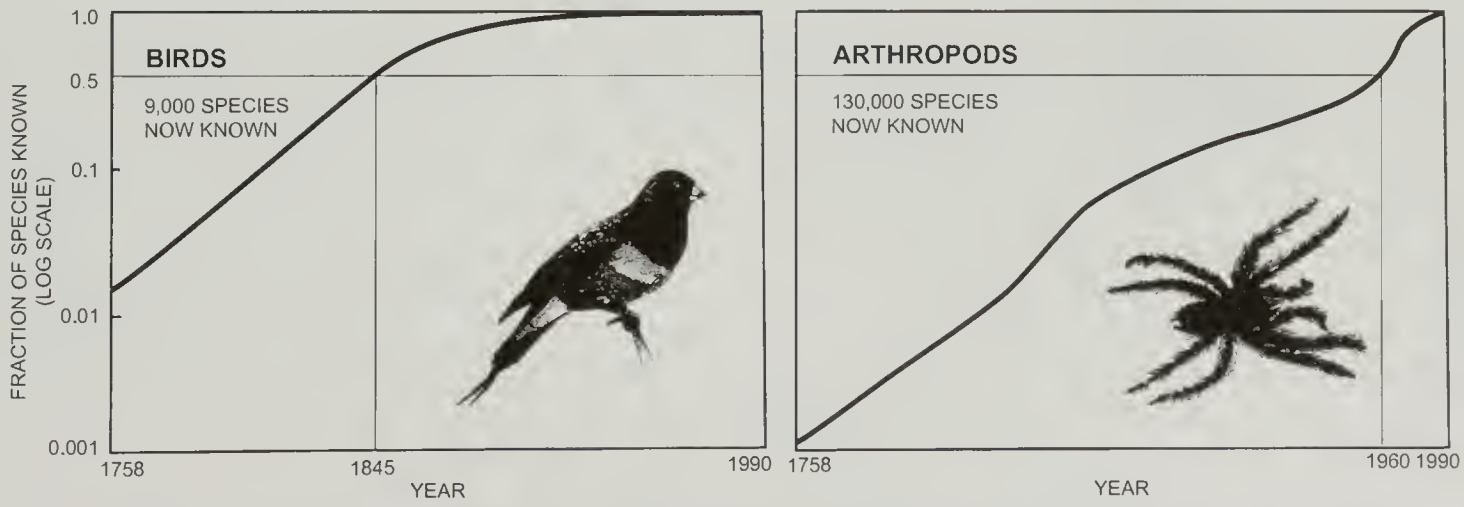

Figure 1. The rate of discovery from the time of Linnaeus (1758) up to 1990. Accumulation of species for a vertebrate representative group, birds, versus arthropods (excluding Insecta) expressed as a fraction of those known in 1990 on a logarithmic scale plotted against time. Note that half of all known birds were already described by 1845, in contrast to 1960 in arthropods. Modified from May (1992).

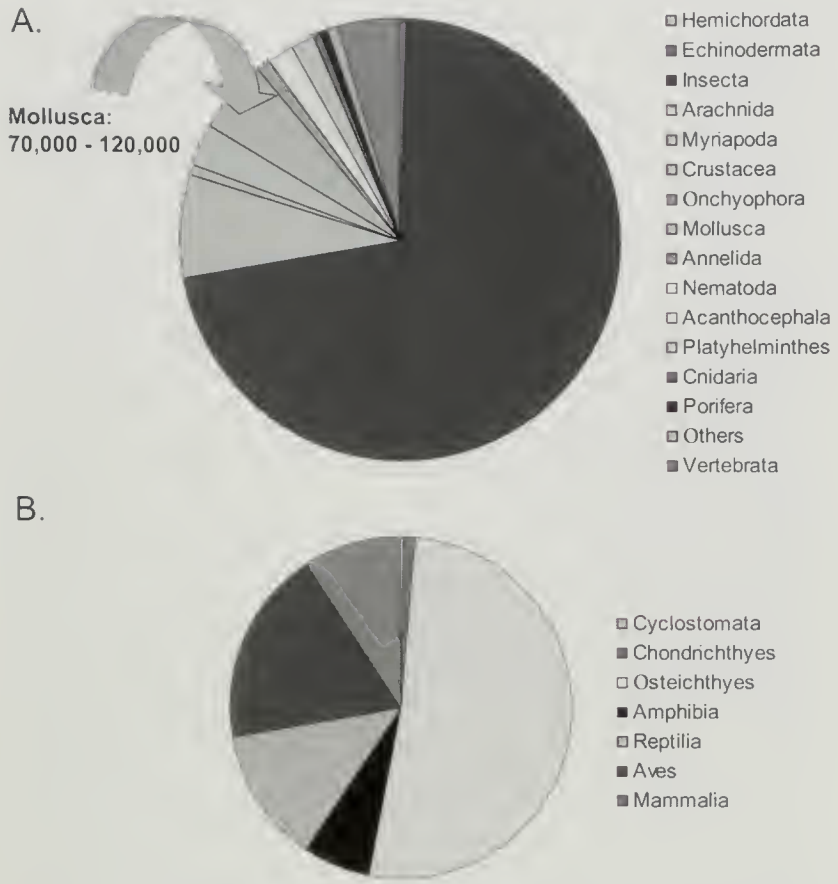

Figure 2. Numbers of known animal species: A, all major taxa; B, vertebrates. Note that for Mollusca the figures is given as 70,000 known species, with the most recent estimate of 120,000 species total. Modified from Chapman (2005).

synoptical and coordinated catalog or compilation exists, nor is any effort made to comprehensively list all named species, in particular for invertebrates. This situation basically leaves us with the *Zoological Record* as the only (albeit with an omission rate of over 20% of new molluscan names) far from complete compilation of supra-specific names (Bouchet and Rocroi 1992, 1993, Edwards and Thorne 1993). It has been suggested to separate this registration of all new names and nomenclatorial acts from the scientific content of taxonomic papers (Minelli 2003a). However, recently the ICZN has set up a new system, called ZooBank, that requires species descriptions to be registered online (Polaszek 2005). Bouchet and Rocroi (1992, 1993) also suggested that names should be registered before they are declared available.

Inventorying the malacofauna

Molluscs as the second largest animal phylum are not an exception to this Linnean challenge as outlined above, with exact figures on the number of living and/or fossil species lacking and extrapolations widely variable. Linnaeus in the 10th edition of his *Systema Naturae* in 1758 described among the 4,236 animals listed (there were 549 species in his first edition of 1735) nearly 700 species of molluscs (listed under "Testacea" that also included brachiopods). Half a century later, Lamarck assumed in his classification 135,000 species of known invertebrates (Laurent 1997).

One of the earliest attempts to more precisely extrapolate the number of living species for all classes of animals from representatives in museum collections was done by the director of the Berlin natural history museum, Karl August Möbius (1825-1908), as detailed in Glaubrecht (2008c). In 1898, using the roughly 30,000 species (with an estimated number of 300,000 specimens) then extant in the Berlin collection (albeit at that time still united with the brachiopods), Möbius arrived at the very conservative figure of 50,000 known species of molluscs (out of or among the well over 400,000 species in total that he at that time estimated). More than half a century later, using instead the available compilations of generic and subgeneric names, Franz Alfred Schilder (1896-1970) tried to estimate at least for prosobranch gastropods, one of the major classes, the number of fossil and extant families. For this subclass alone, he estimated 415 families and about 20,000 genera, a total of 150,000 species (Schilder 1947). He later extrapolated the number of all living molluscs as 250,000 species (among an estimated 3 million animal species), assuming that about half of all species were described at that time (Schilder 1948, 1949).

Later, Muller and Campbell (1954) gave the total number of known molluscs species as a much more reduced 73,000, of which over 41,000 (57%) are living species and over 31,000 (43%) fossil species. Later, Boss (1970) doubted the total of 107,000 living species, with 58,000 marine, 14,000 freshwater, and 35,000 terrestrial molluscs estimated at that time (Nicol 1969). Boss (1971) arrived at only about 35,000 species of molluscs known and, guessing the number yet to be described, he suggested a total of nearly 47,000 molluscan species (with 37,500 gastropods and 7,000 bivalves), later corrected to about 60,000 Recent species.

As noted earlier (Bouchet 1997) molluscs are a group where the number of described species is problematic, ranging from 45,000 to 150,000. For example, May (1990) gave the estimated number of species in this group recorded scientifically to 1970 as 45,000, with 1887 to 1899 being the peak for discovery of new species. According to his estimates, it has taken over 70 years prior to 1970 to record the second half of this total number of 45,000 species. However, May (1988) listed Mollusca with about 100,000 recorded species, estimating the research effort devoted to molluscs (from the average number of publications per year in the *Zoological Record* from 1978 to 1987) as comparable to Lepidoptera and Hymenoptera, but an order of magnitude less than in birds or mammals. Baillie *et al.* (2004) gave a total of 107,718 described molluscan species (75,000 gastropods, 30,000 bivalves, 768 cephalopods, and 1,950 others). These estimates are closer to the one given in Chapman (2005), who arrived at an estimated number of 120,000 species. However, Ponder and Lindberg (2008) tentatively figured that there might be 200,000 extant

molluscan species. For marine molluscs alone, Bouchet (2006) estimated 52,500 species worldwide.

However, as assessments of species richness are confronted with a plethora of difficulties, reliable figures are still wanting. Only rarely are surveys on mollusc species available to date, even for particular classes or larger subgroups. Therefore, we can only roughly extrapolate where the species in Mollusca are, *i.e.*, which molluscan taxa hold how many described species. Using various catalogues and checklists as well as the *Zoological Record* for taxonomic papers (although the later is not without its deficiencies), Bouchet and Rocroi (1992, 1993) compiled the nomenclaturally available genus-group names for the classes of all Mollusca and Recent Mollusca that were introduced since Linnaeus' time (1758) until 1989 (Fig. 3). While cephalopods dominate the fossil record with ca. 34% of all named molluscs, bivalves make up ca. 17% among the living taxa. Depending on the method, Bouchet and Rocroi (1992) found between 25,000 and 28,000 supra-specific names, with nearly half of them (all Mollusca) or two thirds (among Recent Mollusca only) for gastropods. They gave the number of genus-group names of Recent molluscs at about 12,000. Before their compilation, Schilder (1947), in his attempt to estimate the number of species in prosobranchs, suggested that there might be 20,000 genus-group names for all Molluscs, with some 5,000 taxa still being extant while Vaught (1989) arrived at 15,000 genus-group names. With an average of 224 new genus-group names per year, the annual increment has remained relatively stable for molluscs since the late 19th century, thus mirroring the same increasing rate of discovery described by May (1990, 1992) for other invertebrates (Fig. 1).

Several compilations I found in the literature exhibit this pattern. Thus, with respect to molluscs we surely continue to live in the golden age of discoveries, with a plethora of new species yet to be found and described. As only one of the many cases stated here, we continue to do this for a small group of freshwater gastropods endemic to the island of Sulawesi (Rintelen and Glaubrecht 2003, Rintelen *et al.* 2007). Bouchet (1997) figured this progressing species inventory in selected groups of Recent molluscs, among them a few groups of marine gastropods, land snails and bivalves (Fig. 4A). The same general trend can also be seen in the data compiled with a much more restricted focus, for example, by Vermeij (1999) for species with shells having a labral tooth although there are two peaks in the number of described species (Fig. 4B). Here, we have charted the progress of knowledge on two randomly picked groups of molluscs, also using Linnaeus and 1758 as starting point, figuring the cumulative number of known species over the subsequent centuries (Fig. 5). As is evident from these data compiled here for Cephalopoda and *Conus* Linnaeus, 1758, both taxa reveal the one trend already discussed above for invertebrate taxa in general versus vertebrates (Fig. 1).

In his compilation, Bouchet (1997) estimated that, on average, 1,395 new species-group molluscs are named each year (69% are fossil species, leaving 430 living species per year), with the number of new marine species described each year increasing by 68%, while the number of new non-marine species decreased by more than 15% over the past three decades. Nevertheless, Bouchet (1997: 1) also saw no sign of leveling off in the inventory of molluscan diversity, concluding that "for the foreseeable future, micromollusks, the deep-sea, and the marine and non-marine tropics will remain effectively inexhaustible reservoirs of undescribed species". Actually, there is evidence of hitherto unrecognized taxonomic groups among molluscs from all biotopes. Thus, an inescapable conclusion emerges about a largely uncharted biosphere, and that we are still far from having completed the catalogue of life. However, not only are many biotas incompletely studied, but also our lack of knowledge limits our ability to comprehend and respond urgently to the biodiversity crisis, viz. the loss of many of Earth's species. Only one of the many reasons is certainly that institutional and financial support for systematics and natural

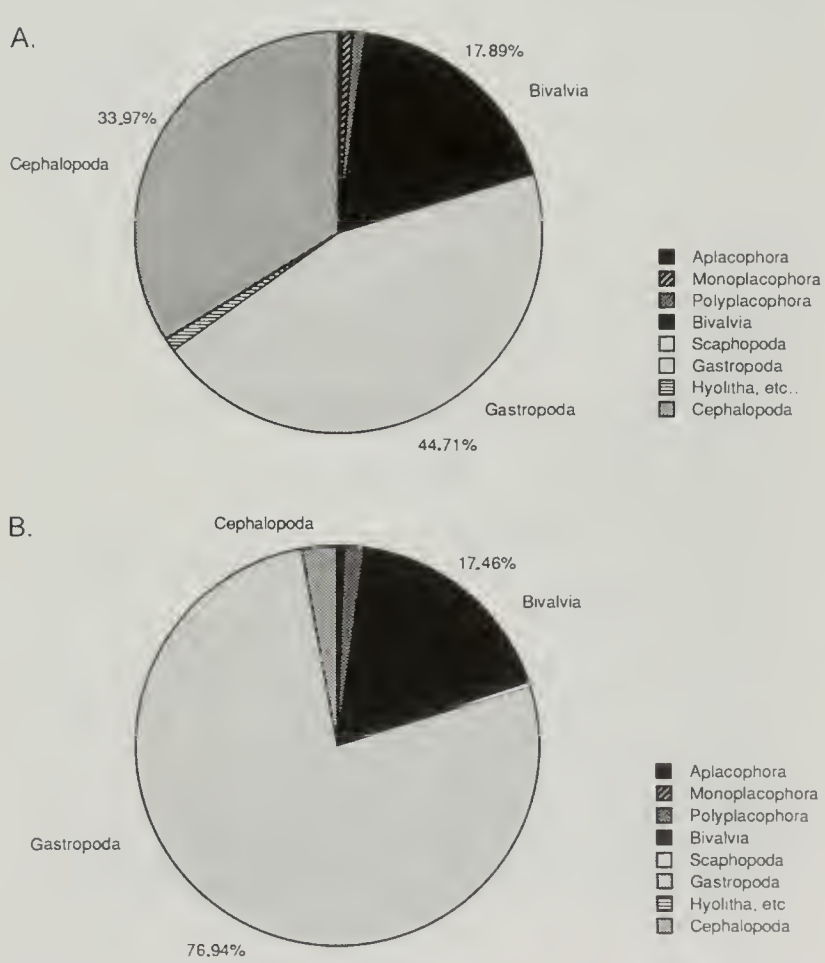

Figure 3. Where are the species in Mollusca? A, genus-group names of all Mollusca, introduced since 1758 (until 1989), partitioned by class, with percentage given for main taxa. B, genus-group names of only Recent Mollusca, introduced from 1758 to 1989, partitioned by class, with percentage given for main taxa. Both figures modified from Bouchet and Rocroi (1992).

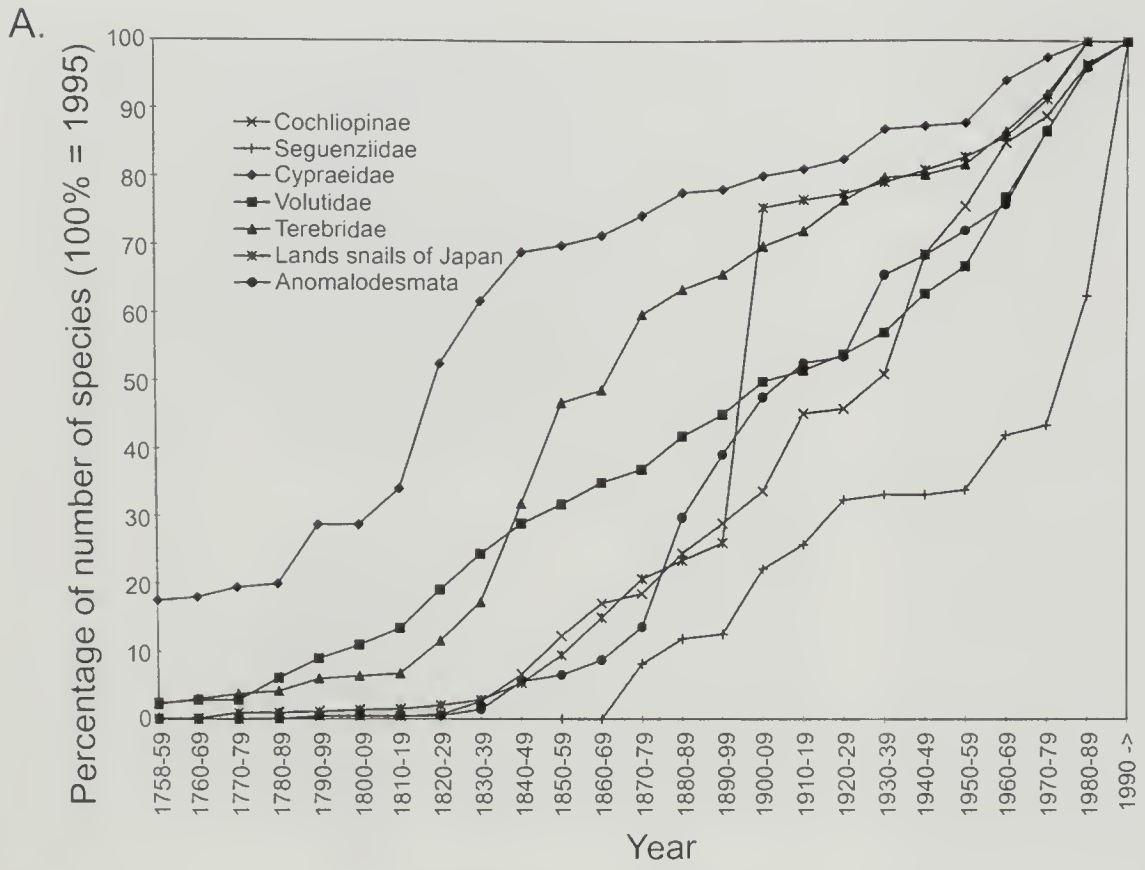

Figure 4. Inventorying the malacofauna. A, number of species of selected molluscan groups since 1758, plotted as a percentage of the known number of species in 1995 (from Bouchet 1997). B, number of gastropod species with a labral tooth described per 20-year interval from 1740 to 1999 (from Vermeij 1999).

history studies have continued to dwindle for several decades now, resulting in a situation called the "other" taxonomic impediment (Evenhuis 2007). At the same time, there have been various claims that this situation will require a fundamental restructuring of the way we do systematics (Godfray 2007), and calls for accelerated biodiversity assessments, in particular suggesting molecular taxonomy (and DNA barcoding) as the proper way out (see below). I claim that this barely faces the real and fundamental problems, as there are still other Darwinian mysteries involved that are not tackled or solved by this approach. These problems center on the question if species are real and how many are valid.

(2) The mystery of the species concept: "*Defining the undefinable*"

May (2004) noted that detecting new species in the field will remain the rate-limiting step to tomorrow's taxonomy. Species are life's mosaic across space and time. However, there is a fundamental disagreement among systematists of all kinds and expertises about what these species are and what we can regard as the functional unit in evolution on the one hand and in taxonomy on the other hand. Searching for biologically meaningful entities, *i.e.*, species as they are conventionally called, as well as how to define and delimit them has been a century-long challenge, and its full understanding needs to take into account an equally long history which cannot even be outlined here. Discussions of the species problem litter the scientific literature, hampering progress, often obscuring a clear vision of the conceptual issues and practical problems centered around species, with this distinction not being always clear-cut. However, the species problem still remains fundamental, irrespective of the common conjecture of it being merely a question of semantics.

Although the question "what is meant by a species?" cannot be pursued

here in more detail (see Bock 2004, Coyne and Orr 2004, Glaubrecht 2004, Reydon 2004, Hey 2006, Stamos 2007, Samadi and Barberousse 2006, 2009), a few remarks should be made on the understanding (and often enough misperception) of what earlier, influential systematists and evolutionary theorists have thought about the nature of species and why this is of relevance in particular today. Astonishingly, the species problem is not only regarded as being an old one, but it is often erroneously concluded from this fact that the species question is either irrelevant or problematic (Noor 2002) and, thus, should be avoided. I completely disagree and anticipate that this perception is at least as fatal as our lack of knowledge of species numbers.

Firmly convinced about the divine origin of nature and the stability of species, for example, Carl Linnaeus and his followers during the subsequent century believed that "*species tot sunt quot diversas formas (in principio) in initio produxit infinitum eus*", *i.e.*, there are so many species as God has created in the beginning (Blunt 2001: 266). Under this assumption, delimiting species was only a matter of describing the most relevant (*i.e.*, morphological) features for identification and classifcation. However, during Darwin's time it became a widely realized problem of how to define the "undefinable", as the species problem is called. It has repeatedly been erroneously referred to in the literature that Darwin, after having struggled long with the species question, applied a somewhat cynical definition of species being merely what "competent naturalists" say they are. Several statements in Darwin's work seem to prove this view on his confusion over species that many systematists and evolutionary biologists commonly hold (Mallet 1995, 2008a, 2008b, Stamos 2007). However, it seems worth noting that Darwin's species concept changed, for sound reasons, since the time when he started his early notebooks on the transmutation of species in 1837 and publishing his "*Origin of Species*" in 1859. As Kottler (1978) and Sulloway (1979) have shown in great detail, Darwin clearly subscribed to the reality of species and identified the acquisition of reproductive isolation as a mark of completed speciation, irrespective of his later statements on species as arbitrary

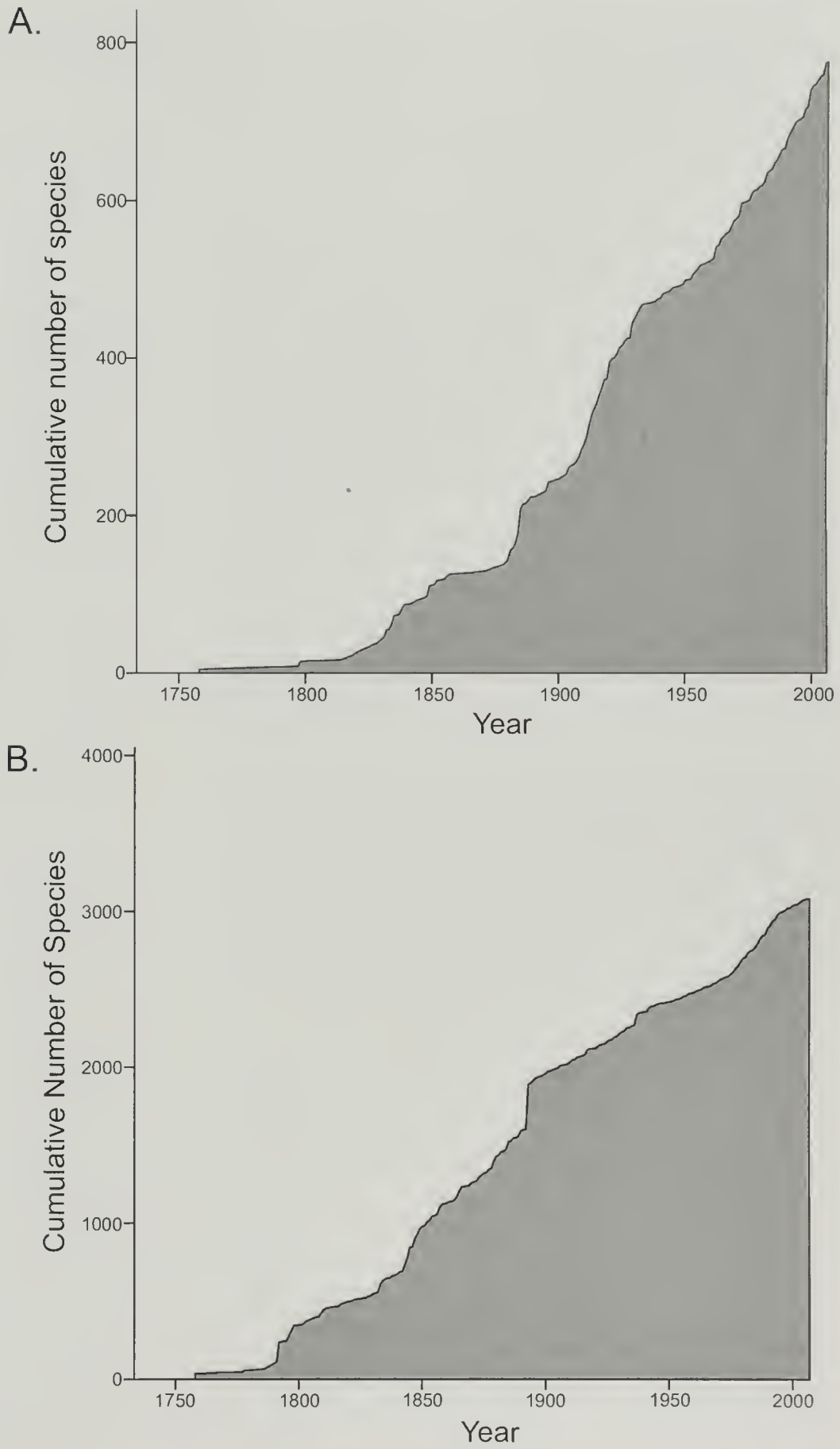

Figure 5. Increase of described species in Cephalopoda and in *Conus*, revealing one trend in two randomly chosen taxa. A, cumulative species number in Cephalopoda, 1758-2006, with species currently considered valid (modified from Wood and Day 2006, Cephbase as of July 2007). B, cumulative species number in the neogastropod *Conus*, 1758-2007, with available species names given (modified from Kohn and Anderson, 2008, *Conus* Biodiversity Website as of July 2007).

constructions of taxonomists in relation to his new evolutionary theory. This discussion and the Darwinian dilemma on the duality of species as a taxon and concept remain today, in particular with the practical procedure of how to delimit species with the availability of new tools.

The reality and duality of species

In many respects, modern research has returned to some of Darwin's original interpretations, as Hendry (2009) stated, referring to the most recent perceptions propagated by Mallet (2008a, 2008b). Ernst Mayr (1904-2005) with his 1942 synthesis a watershed in the history of the species-problem, triggered a new age of this debate when elevating several different approaches to species identification to the level of concept (Hey 2006, Glaubrecht 2007, Mallet 2008a, 2008b). Mayr's biological species concept surely remains a highly useful approach to the study of species and speciation. Evolutionary biologists, in particular those who study the pattern and processes of speciation (see below), believe that species of sexually reproducing organisms are real (*i.e.*, they exist without us to assign them) and that they exist by virtue of reproductive isolation rather than phenotypic distinctness (Mayr 1996, 2001, Coyne and Orr 2004, Glaubrecht 2004, Hendry 2009). However, as is clearly evident from the vast literature still being produced on this subject, the species problem has still not been adequately resolved from its empirical and practical aspects as well as its philosophical perspective. Persisting misconceptions as to the nature and importance of species, in particular the permanent confusion of *species taxon* with *species concept*, hampers both biodiversity research and understanding evolution, leading to pertinent problems with merely artificial delineation and naming of species.

In light of the many proposals of species concepts, which have become almost a cottage industry, Bock (1995, 2004) and Mayr (1996, 2001) have explained that there is a fundamental distinction as to this duality of species as category and concept. On the one hand, there is the practical procedure of how to delineate a described taxon as a species within a taxonomic category of the Linnean hierarchy; on the other hand, there is the theoretical concept of species using objective criteria, as *e.g.*, defining species based on reproductive isolation. As species concepts (the meaning of species in nature) and species taxa (as zoological objects to be categorized in an ordering system) are different things, we need to clearly differentiate between *describing* species and *defining* species. As pointed out before (Glaubrecht 2004), these two sets of species problems are often ignored, in particular with respect to the description and identification of species, *i.e.*, the question of the delineation of species as a practical procedure using operational and empirical criteria. Unfortunately, recently it is largely this latter, operational aspect (how to delimit species using new molecular tools, rather than what it actually represents in nature) that has been focused on (Sites and Marshall 2003, 2004, Agapow *et al.* 2004, Samadi and Barberousse 2009).

As much as these procedures are important, I would argue that having a clear idea what species are remains essential. In malacology, for example, naming nearly every conchologically distinguishable specimen or population in the typological manner of the 19th century has been misleading (Glaubrecht 2000, 2004). As argued there, our task is not to find the least distinguishable unit but to make meaningful inferences on the existence of evolutionary entities in nature. In terms of testing of the null hypothesis of typology (*i.e.*, what looks different is different), we need to strive for identifying not only arbitrarily delineated taxa but also specific entities with their own evolutionary trajectories, using all available biological data including the reproductive criterion of the biospecies concept as well as relevant morphological, molecular genetic, geographic, and other data. Irrespective of the enormous use of molecular markers in systematics, phylogeny, and phylogeography (Avise 2004, 2006), it is worth realizing that as much as morphology can only be used as a proxy to phenotype, molecular sequence differences are not more than a far less reliable proxy to the genetic history of a given taxon.

Currently, with about two dozen species concepts around and in view of the ongoing confusion of species concepts and species taxa (see above), the theoretical foundation of any biodiversity approach is weak. At the same time our understanding of the nature of species has, of course, fundamental implications for evolutionary biology and historical biogeography. Thus, it still is a relevant task to establish if and where the concept of biospecies is applicable or if we need to find and define new and improved concepts. In any case it will be necessary to implement a common language for all biodiversity assessments, *i.e.*, to specify those units that are used in individual approaches. As much as it is claimed by proponents of the practice of DNA profiling of animal taxa (see below) that species are recognizable by sequence variation as groups of close relatives, the idea of finding and applying statistical generalities for species differentiation is fallacious. Eventually, it needs to be established whether all units currently used, including MOTU ("molecular operational taxonomic units") but also, *e.g.*, chronospecies in the fossil record, carry meaningful information in the global task of a bio-inventory in space and time.

Therefore, reiterating an earlier plea (Glaubrecht 2004), we should explicitly say what we mean when dealing with the species question, for example, which species concept we want to apply and for what reason. As crucial as diagnosing and demarcating species are, only if we understand the nature of species and define more properly the various levels of evolutionary units, can we arrive at meaningful conclusions for

evolutionary biology and biological diversity. It will be the challenge of modern biosystematics to review the various approaches and develop unified strategies for the verification of these units of evolution as a major principal theoretical component, not only for biosystematics but also for any biodiversity assessment and evolutionary biology in general. In the following, I will only discuss a few aspects relevant to this task.

Taxonomic redundancy: Which of the nominal species are real?

The history of taxonomy and of malacology in particular teaches us that there have been many specimens, populations, or taxa named, thus immortalized until later often synonymized. Undoubtedly, superfluous or duplicate names for species as biological entities have been introduced repeatedly, at all times and in all taxonomic groups. Thus, in particular the taxonomic literature for invertebrates often deals with names only but not real species or biological entities. This problem of unresolved synonymies might generally be widely known, but its resolution has not been attempted systematically, hampering many scientific hypotheses ranging from biodiversity assessments to speciation theory, models for radiation, and historical biogeography.

Actually, only rarely has the degree of taxonomic redundancy that inflates species number estimates been derived from any compilation of catalogues and checklists (see, however, for insects Solow *et al.* 1995). Alroy (2002) studied this bias by comparing historical rates of invalidation and revalidation of named species using taxonomic data of unrivaled completeness for North American fossil mammal species. From analyzing how many named species remained valid, he concluded that diversity estimates are inflated by 32-44% for the taxa under study (Fig. 6), arguing that this is a conservative figure compared to other methods. Most importantly, Alroy (2002) suggested from several lines of evidence that the same bias probably affects more poorly studied, hyper-diverse living groups, such as insects and, as I anticipate here, also molluscs. As we have to expect substantial inflation of total species counts everywhere in the literature, Alroy suggested that current estimates of total global diversity should be revised downwards to as low as 3.5 to 10.5 million species, if a third of named species are a reflection created by unsettled taxonomy. Others have argued that his optimistic estimation of fossil coverage, while ignoring the vastly different techniques used to delineate species in living and fossil taxa, render such an extrapolation meaningless (Agapow *et al.* 2004: 168). Nevertheless, May and Harvey (2009) estimated that with synonyms removed, the total number of known animal species that is currently assumed to be 1.8 to 1.9 million, may be 1.6 million or fewer.

For molluscs, though, a level of taxonomic redundancy that is twice as high as this latter estimate and in the range of Alroy's figure might be likely. Schilder (1949) estimated that 34% of the names available to classify prosobranchs were synonyms. He found that 49% of the names that were established in the first half of the 19th century were synonyms, with the synonymy ratio decreasing to 37%, 34%, and 21% respectively for the next consecutive quarter-century intervals. As Bouchet and Rocroi (1992: 84) suggested, this is either the result of taxonomists doing better work since the early 19th century or indicates that it takes many decades to assess the value of a given name. That many molluscan species names are synonyms was also assumed by Boss (1970) who estimated that the synonymy ratio (*i.e.*, the number of available nomina for the number of actual species) averages 4:1 to 5:1, suggesting that a single species may have on the average four to five names in molluscs. His guess was certainly driven by extreme cases like the European swan mussel *Anodonta cygnea* Linné, 1758 with over 500 names. Bouchet (1997) found, based on a small subsample of his data, a synonymy ratio of 1:6. Extrapolating from the assumption that of the average number of 430 molluscan species described as new each year, only 265 are actually valid, we can calculate a synonymy ratio in molluscs to be as high as 38%, or that 62% of the new species described in the last few decades are indeed new species (compare this, for example, to insects with an estimated inflation rate of 28%, Alroy 2002).

It would be interesting to thoroughly investigate the influence of revised biological concepts such as that of what a species is and how we define and delimit it (see above) on our diversity estimates, as discussed by Boss (1978) for bivalves and for freshwater cerithioidean gastropods in Glaubrecht (2004). As I argued, such a study would be all the more timely,

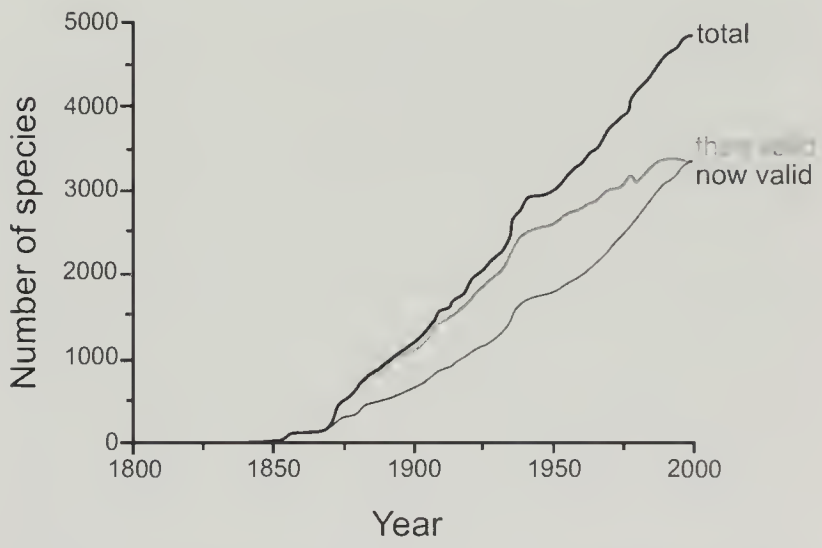

Figure 6. How many named species are valid? Growth through historical time in the number of all named species compared with those considered valid at a time and thought to be valid today. These data from North American fossil mammals suggest diversity estimates are inflated by 32-44% (from Alroy 2002).

since the increasing application of merely phylogenetic species concepts, that name least distinguishable units instead of biologically meaningful entities, will contribute to the taxonomic inflation.

The only study explicitly to review in a comparative manner the influence of, for example, the phylogenetic species concept (resting on the idea of diagnosable differences) versus the biological species concept is hopelessly flawed in respect to the only three examples stated for molluscs, given that one of the three studies cited in Agopow *et al.* (2004: 167, table 1) is actually a deep-sea shrimp, while the other two deal with only two species under the BSC (biological species concept) versus one under the PSC (phylogenetic species concept). Apart from the doubtful relevance of these cases, this reverses (as the perplexed authors stated) the commonly expected trend they otherwise found in their study, that surveys based on the PSC lead to recognition of a far greater number of much less inclusive units. Accordingly, under the PSC we would end up with 48% more "species", which has serious consequences not only for conservation and biodiversity (as it will shift identifying taxa and regions of biodiversity) but also for all biology. Again, however, for molluscs what we know is from very few samples, and what we need is a systematic survey on this taxonomic redundancy and inflation.

Taxonomic inflation: In search of the "new" species diversity

In general, biodiversity is synonymous with the number of species (at least in neonotology, as paleontologists count numbers of genera or even families, which are artificial hierarchical categories, not natural entities). Consequently, if species were used as a proxy for diversity, not only the theoretical understanding of these units becomes essential for all conclusions, but their number itself. Recurrent discoveries using more advanced molecular genetic techniques suggest a plethora of cryptic species and thus hidden diversity, implying that we might largely underrate organismal diversity (Bickford *et al.* 2006, Pfenninger and Schwenk 2007), possibly including molluscs.

Clearly, gene sequence information for many taxa has contributed to the ascendancy of phylogenetic over biological species concepts. However, any kind of taxonomic inflation, *e.g.*, when known subspecies are raised to species as a result in change of species concept rather than new discoveries, also has important influences on many fields in biology. It will, for example, result in re- and sub-classifications, heat up biodiversity hot spots, and lead to devaluation if the smallest distinctions are raised up to the level of what makes a species (Agapow *et al.* 2004, Isaac *et al.* 2004).

Next to the adoption of the PSC over the BSC as most recent development in this context, the application of routine methods in molecular taxonomy (such as DNA barcoding) have contributed immensely to the view of biodiversity being underestimated. Undoubtedly, for a long time the lack of obvious morphological differences between taxa has impeded the identification of species in many groups of animals including molluscs. Currently, molecular species identifications boost species diversity figures in all parts of the tree of life (Blaxter 2004, Lee 2004, Savolainen *et al.* 2005, Köhler 2007, Vogler and Monaghan 2007, Meier 2008). Given the increasing armamentarium of molecular genetic techniques for exploring the genetic structure of populations, species, and higher level taxa, not only do we uncover further complexities in what we mean by a species but also we are confronted with modifying and/or adopting the species concepts used to evaluate the level of taxonomic and biologically relevant diversity (May 1990). I have discussed this for freshwater certhioidean species diversity elsewhere (Glaubrecht 2000, 2004).

Although more thorough comparative studies in concert with systematic revisions are lacking to substantiate this claim, there are cases to support the caveats. For example, Meyer and Paulay (2005), using cypraeid gastropods, showed that the much-debated barcoding approach works well only for species that are already well studied but is hardly an instrument for accelerating species inventories, as there is not a certain and universal threshold. Tackling the "barcoding gap", *i.e.*, using different means in intra- and interspecific sequence variability for congeneric COI sequences to distinguish between taxa (Meier *et al.* 2008), Köhler (2007) discussed for pachychilid gastropods the largely overlapping intra- and interspecific genetic variation. Using uncorrected p-distances in COI that vary between 0.0 and 0.11 within, and 0.0 and 0.16 between species, he also pointed out the variation even among congeners, which argues against the acceptance of threshold values to postulate species identity, as DNA taxonomy promises something that it cannot deliver. A most striking case is reported by Dillon and Robinson (2009) who found extremely high intra- and inter-population sequence divergence in "living fossil" pleurocerid gastropods from the Appalachians, ranging more than 22% within and between populations, respectively. Using any kind of threshold is a license for splitting over lumping but will not provide answer to the essential question of the genetic integrity of species in nature.

Nevertheless, DNA techniques certainly help as an identification tool, *e.g.*, in marine larvae, or where traditional techniques underestimate species diversity, such as in microscopic animals, or to identify complex phenomena such as the existence of cryptic species complexes, particularly in hyperdiverse taxa, morphologically very similar taxa, or in young radiations. Recent cases from molluscs are marine *Conus* (Duda *et al.* 2008), the vermetid *Dendropoma* Mörch, 1861 (Calvo *et al.* 2009), or species complexes in calyptraeids (Collin 2000, 2005) as well as freshwater *Bythinella* Moquin-Tandon,

1856 (Bichain *et al.* 2007, Haase *et al.* 2007, Benke *et al.* 2009), and the (presumably truly adaptive) radiation of *Tylomelania* Sarasin and Sarasin, 1897 on Sulawesi (Rintelen *et al.* 2007, Glaubrecht and Rintelen 2008).

Currently, large-scale DNA sequencing provides new opportunities for the study of species and speciation. However, single short mtDNA gene fragments, as in the barcoding approach, should be used for classification and systematics only if placed in a wider phylogenetic context. Since sequence divergence in itself is an extremely crude method for determining species limits, it is the plurality of systematics tools (including morphological, biogeographical, ecological, and ethological) that needs to be employed in concert. Molecular taxonomy such as DNA barcoding should no longer try to bypass traditional taxonomy but be integrated within and done in concert with relevant systematic knowledge and practices. However, as Isaac *et al.* (2004) predicted, as practically oriented species concepts such as the PSC gain popularity, in particular among molecular taxonomists, the resulting taxonomic inflation will affect more taxa, any biodiversity survey, and even evolutionary studies and hypotheses. It will be interesting, if we will eventually witness this current trend from splitting to lumping to reverse again. As we will only be able to understand biodiversity and evolution fully once we know what species are and how many there are, both issues are of eminent importance and not fully reflected yet in our research activities.

(3) Speciation: Darwin's "*mystery of the mysteries*"

As much as of species themselves and their roles in taxonomy and ecology, a better understanding of speciation is not just an academic exercise but crucial for evolutionary and biodiversity studies. Of course, only if species are real, does the process of speciation become a real process and the study of their formation and transformation become a meaningful scientific endeavor (Glaubrecht 2004). Speciation, as the process of how new species evolve, eventually results in the multiplication of species; thus, speciation is the major factor causing biodiversity and is also fundamental to our understanding of evolution. As much as the debate on what species are has created confusion and controversy for a long time, so has the process that brings species about been discussed. Therefore, speciation remains at the forefront of current evolutionary biology (Mallet 2008a, Nosil 2008, Schluter 2009).

Unfortunately, too often taxonomists feel that describing any assemblage of species (living as well as fossil taxa) already justifies the term "speciation" in the titles of their publications. The subject of speciation, though, is much more than just an assemblage of species names. With respect to the above-mentioned "big questions" raised for the near future of biological sciences, studying the underlying mechanisms of diversity still remains a most fascinating subject.

Toward solving Darwin's mystery

In this context, it is important to realize the two main focal points of evolutionary biology, namely anagenesis (natural selection acting to transform existing taxa) versus cladogenesis (the actual multiplication of species). While Darwin's (1859) work is acknowledged as brilliant induction, presenting insightful examples of adaptation and anagenesis, Mayr's (1942) synthesis provided an explanation for cladogenesis, grounded chiefly in geography, largely ignored before. Thus, our current understanding of how species multiply was influenced by Mayr's credo that geographic distribution and spatial isolation play a key role in allopatric speciation, as in the course of the Modern Synthesis of evolution it became firmly established that geographic separation is a major factor in speciation (Mayr 1982, 2001, Coyne and Orr 2004). Glaubrecht (2002, 2007) reviewed the historical avenues and intellectual roots, including the contributions of German systematists of the "Berlin School", built by Erwin Stresemann, Bernhard Rensch, and Ernst Mayr. Their "New Systematics" was regarded as crucial for providing, in the 1920s and 1930s, the foundation for synthetic evolutionary theory.

In the last decade, however, it became apparent that although allopatric speciation is important in many cases, it is not the only mechanism and might not even be as important in evolution as Mayr was convinced throughout most of his long life. It became evident recently that an ecological rather than geographical explanation may account for how new species come into being. A key feature of sympatric speciation (Bolnick and Fitzpatrick 2007), ecological speciation by adaptive divergence is an engine of speciation. Accordingly, as assumed implicitly by Darwin, natural selection and adaptation are the means of generating biodiversity, particularly in the context of adaptive radiation (Schluter 1996, 2000a, 2000b, 2001, 2009, Orr and Smith 1998, Sudhaus 2004, Rundle and Nosil 2005, Hendry 2009, Nosil *et al.* 2009). Instead of geography, factors such as phenotypic plasticity, intra- and interspecific competition, with character displacement and specialization, lead to divergence and eventually to speciation. Thus, with ecological speciation as a major player in the diversity of life, allopatric versus sympatric speciation remains one of the most conspicuous current battlegrounds in evolutionary biology.

This central controversy is far from being settled as it is not resolved yet what genetic chance will result in a new species, and under which conditions, thus what the true influence of genetics, geography, and adaptation on speciation is. With new genetic research and genomic techniques homing in on the molecular and cellular mechanisms that enable diversification to occur, our current understanding of the speciation process has improved considerably, allowing us to answer to the next generation of questions on the frequency and importance of different processes that cause speciation

(Noor and Feder 2006). In this context, the long debated phenomenon of interspecific hybridization, a major focus for evolutionary biologists since Darwin, has gained attention lately (Seehausen 2004, Mallet 2005, Schwenk *et al.* 2008). Hybridization and introgression, with various levels of gene flow, in the absence of strict allopatry are antagonistic to the process of speciation but, nevertheless, might play an important role in adaptive radiation (Seehausen 2004, Gavrilets and Losos 2009).

Using molluscs as models

Molluscs certainly can contribute to these highly interesting and controversial subjects of speciation mechanisms, such as hybridization and adaptive radiation. For molluscs, however, we lack textbook examples for sympatric and ecological speciation, adaptive divergence, and hybridization, such as provided by Darwin's finches, threespine sticklebacks, or hyper-diverse cichlid fishes. Yet, there are certainly suitable potential candidates, for example molluscs in ancient lakes, from oceanic islands, mountains, or other insular environments with endemic species. It is in this context that we regard the freshwater pachychilid snails *Tylomelania* Sarasin and Sarasin, 1897, endemic to the central lakes on the Indonesian island of Sulawesi (Glaubrecht and Rintelen 2008) and the thalassoid paludomid snails in East Africa's Lake Tanganyika (Glaubrecht 2008a) as being truly "Darwinian snails". Unfortunately, too few studies have been experimentally designed and/or conducted in such "natural laboratories". No attempt will be made here to review those but the papers given during the 2007 WCM meeting in Antwerp, of which some are in the present volume, will certainly indicate how much malacology currently contributes to these issues.

As was shown by Schwenk *et al.* (2008) in their introductory overview on hybridization, not only has the number of publications risen enormously during three phases (from up to the 1990s, from 1991 to 2002, and since 2003), with the third phase driven by the availability of multiple nuclear markers, *i.e.*, microsatellite DNA, AFLP, and SNP. But, again using the database of the *Zoological Record* (for 1947-2007), they found that, when corrected for taxon bias and taxonomic practice (*i.e.*, organismal preferences of research teams and number of species per taxonomic group), the rate of interspecific hybridization is relatively homogeneous among animal groups, approx. 1%, fairly low compared to predictions of about 10% on average in animals (compared to 25% in plants, Mallet 2005). Consequently, for mollusc species we have *a priori* the same chance for finding and studying this evolutionary phenomenon as in other groups where of course, birds, butterflies, and mammals again take a lead. However, as in the case of the term "adaptive radiation" (Glaubrecht 2008b), too often malacologists continue to use evolutionary issues for their paper or book section titles in lieu of a soundly designed study. Instead of perpetuating an outdated concept (inferring adaptive radiation from the taxonomic description of any speciose group), we should investigate with adequate and timely methods founded on solid theoretical background the underlying mechanisms of anagenetic and cladogenetic change.

As evolutionary biologists working with molluscs, we should test the universality of the known and discussed speciation mechanisms. To date, these are essentially applied to vertebrates (mostly to birds and fishes), but remain largely untested for various groups of invertebrates with the notable exception of butterflies and dipterans among the insects. It is with a clear focus on the above-mentioned mechanisms, however, that we should choose our molluscan models to increase the frequency with which we utilize them as a source of data for studies on speciation, adaptation, hybridization, and radiation, in order to help decipher the underlying mechanisms of biodiversity.

(4) Biogeography: Where are the species and why are they distributed there?

Since the time of Darwin and Wallace, biogeography was at the forefront and at the same time an integral part of further developments in evolutionary biology. Despite centuries of noting the occurrences of animals and plants and the establishment of biogeography as a scientific discipline in its own right (Glaubrecht 2000), we have too few data on distributional patterns for most invertebrates, with, unfortunately, the majority of molluscs being no exception. Nevertheless, it would be easy for us to change this situation. Using more molluscs as model cases would immediately result in an increase in contributions toward this discipline, as is indicated by papers published in *Journal of Biogeography* (Glaubrecht, unpubl. data). For example, in 1980-2000, a total of 345 taxa-related titles yielded the frustrating rate of only 7% being dedicated to Mollusca, with 80% on non-marine taxa (Fig. 7). On the other hand, our contributions to a symposium on the biogeography of SE Asia in 2000, explicitly employing freshwater gastropods as models, resulted in a share of 28% (out of 25) of the taxa-related papers given. Similar results have been found in a recent review of phylogeography by Beheregaray (2008: 3764).

However, aside from noting the data for comprehensive and comparative analyses are generally lacking, I will not attempt to review the existing contributions to molluscan biogeography. Instead, I will only mention the two most recent seminal analyses by Reid *et al.* (2006) and Williams and Duda (2008) as stimulating approaches for future studies of this kind. The former employed molecular analyses of littorinid snails in the central Indo-West Pacific to test phylogeographic hypotheses and showed that species from 'continental' habitats exhibited strong phylogenetic breaks

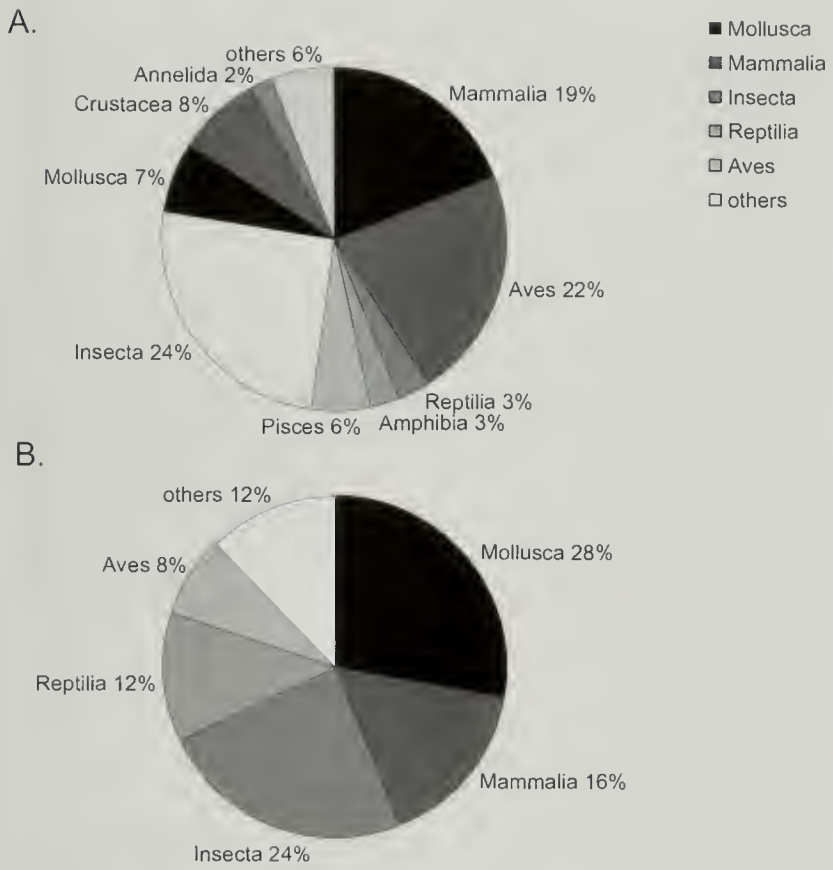

Figure 7. Which animal group is employed in biogeographical studies? A, analysis of papers published in *Journal of Biogeography* in 1980-2000, with a total of 345 taxa yielding a rate of 7% for Mollusca. B, increased percentage of contributions on non-marine molluscs given at a symposium on the biogeography of SE Asia in Leiden in 2000.

between the Indian and Pacific Ocean, in contrast to 'oceanic' species. The latter used analyses of molecular phylogenies of three unrelated tropical marine gastropods, in concert with the timing of plate tectonic events (in this case the collision of the Australia and New Guinea plate with the southeast extremity of the Eurasian plate) during the Oligo-Miocene about 25 million years ago, to show that a speciation pulse occurred in the central Indo-West Pacific at that time.

(5) Phylogenetics: How are species (groups) related?

To Darwin, although helping contemporaries and future generations embrace the common ancestry of organisms on Earth, large parts of the tree of life remained enigmatic. This holds true even today, to the extent that the phylogenetic relationships not only of major animal phyla but also of many terminal branches are still unresolved. Having replaced earlier intuitive ways of finding or subjectively postulating relationships by a clear-cut empirical methodology, it was the German entomologist Willi Henning (1913-1976) who in the 1950s and 1960s single-handedly revolutionized biosystematics. With his guidance, phylogenetic studies were transformed from an art to a truly scientific method, *i.e.*, phylogenetic systematics, creating the basis for a completely new subdiscipline, cladistics (Williams and Forey 2004). It was actually a "silent revolution", as beyond the limits of systematists this new method remained completely unrecognized, with its implications still being underestimated.

Another "silent revolution" took place when phylogenetic systematics was wedded recently with modern molecular genetic methods, first with new sequencing techniques, then with genomic approaches. Albeit those latter developments are too young to be fully applied yet, the contributions in Ponder and Lindberg (2008) provide an up-to-date overview of where we stand 150 years after Darwin in respect to the phylogeny of Mollusca. Currently, even newer advances in molecular genetic techniques (see below) open further avenues for research in systematics, phylogenetics, phylogeography and, thus, the study of evolution.

(6) Genetic causation and molecular processes: How do new forms come into being?

The question of how new forms come into being has long fascinated naturalists. An emerging discipline, called "evo-devo", currently probes how genes involved in development contribute to evolution. It tries to connect developmental and evolutionary biology and to bridge the gap between the genotype and the phenotype, thus linking DNA-focused studies and molecular evolutionary processes with the question of biological diversity and disparity (Carroll *et al.* 2001, Minelli 2003b, 2009b, Carroll 2005, Minelli and Fusco 2008). For an overview in Mollusca, see Wanninger *et al.* (2008).

At the same time, genome sequencing is no longer a pricy luxury done only by few, well-funded researchers on even fewer model organisms. With new technological developments and tools, prices are constantly falling. New methods, such as high-throughput SNP custom cDNA, microarrays, whole-genome and next-generation sequencing (*e.g.*, pyro-sequencing) that can also generate large amounts of expressed sequence tags (EST), are developing faster than ever before, making functional and comparative genomics one of the hottest fields and emerging frontiers of research (Clark 2006, Lee and Mitchell-Olds 2006, Service 2006, Schuster 2008, Wheat 2009). For the current situation in Mollusca, see Simison and Boore (2008).

As eventually malacology will go genomic, the overview in Ponder and Lindberg (2008) provides available phylogenetic knowledge from which we can proceed into this new genomic era. I anticipate that within the next decade the continued exploration of genomes and the study of the molecular underpinnings of any aspect of the phenotype of organisms will give us a better knowledge of the genetic architecture and those genes responsible for form and function in many animals. In reviewing an example of first new insights from the functional genomic study of a *Haliotis* Linnaeus, 1758

species, Medina (2009: 764) noted "that given the, until recently, unimaginable ease with which we can now develop genomic tools for non-model organisms, examining developmental processes in multiple species will be a powerful tool". She concluded that "the transition of comparing a few genes in few species to whole transcriptomes in an even wider range of species will enhance our understanding of the evolution of animal diversity" (2009: 764), as non-model organisms step into the spotlight. Utilizing these new genomic tools and integrating them with evo-devo studies, phylogenetics, ecology, and historical biogeography will greatly change and enrich biosystematics and evolutionary biology in the near future. For both evolutionary biologists and malacologists it is indeed an exciting time—and what a long way we came since Edgar Allen Poe pondered about the soft bodies of molluscs.

CONCLUSION: NEXT GENERATION BIOSYSTEMATICS—A PROGRAM FOR THE FUTURE

As I have tried to show, any biosystematic and evolutionary research on the metazoan level is based on (i) inventorying and describing the basic taxonomic components (*i.e.*, species), (ii) resolving the phylogenetics of the taxa involved (*i.e.*, the genealogical relationships), and (iii) asking questions about the mechanisms of causation, *e.g.*, modes of speciation (*i.e.*, allopatric, sympatric, ecological), including the ecological and developmental constraints, by studying the molecular underpinnings. However, given the lack of knowledge and baseline data, filling these gaps clearly remains the daunting challenge for biological sciences in general and malacology in particular. For quantifying biodiversity, establishing phylogenies, and understanding the evolutionary process of speciation and radiation as well as the taxonomic diversity and morphological disparity, several prerequisites are indispensable, albeit neglected in many modern systematic approaches.

Understanding how diversity is shaped, what species are and how they come into being, where species are distributed and how they are related, will require a major interdisciplinary effort, involving many different kinds of studies. Along the way toward clarifying the history of life we will have to eventually solve the six Darwinian mysteries, which involve inventorying and describing the basic taxonomic components, species, resolving the phylogenetics of taxa by uncovering their genealogical relationships, asking questions about mechanisms of causation on all levels, from modes of speciation to evolutionary transformations, and including ecological data as well as a study of developmental constraints and other genetic factors.

While evolutionary biologists have just started to sort out the most relevant factors intertwined in answering these questions, molluscs with their multitude of morphological, genetic, and ecological features have much to offer. They are a highly suitable group for providing fundamental insights into mechanisms of the genesis of biological diversity and disparity, into historical zoogeography, and into the underlying processes of speciation and radiation, as is also shown in the many contributions to the Antwerp symposium on this subject (Glaubrecht and Rintelen 2009). The myriad of mollusc species offer the material basis for conducting a research program along the lines sketched out above.

We still need to discover many missing bricks in the sense of Henri Poincare's statement used as an epitaph here for this article. Surely, molluscs will not only provide many of the yet missing pieces, but we should also strive to integrate new findings based on this extraordinary taxonomic group into a more comprehensive synthesis of forces and factors influencing biological diversity.

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